

THE SYSTEMATICS OF THE SOUTHERN HEMISPHERE
CHITON GENERA *RADSLIA* GRAY, 1847, AND
SYPHAROCHITON THIELE, 1893
(MOLLUSCA: POLYPLACOPHORA: CHITONIDAE)

Robert C. Bullock

Abstract.—The name *Radsia* Gray, 1847, which has generally been considered to be a junior synonym of *Chiton* Linnaeus, 1758, should be used as a genus-group *nomen* for its originally designated type species, *Chiton barnesii* Gray, 1828, and the South African *Chiton nigrovirescens* Blainville, 1825. Although *Radsia* was at first characterized by its multiple-slit insertion plate, which is not always a reliable taxonomic character, it appears useful to employ the name *Radsia* for these two species that exhibit ancestral shell, radular, and reproductive features reminiscent of certain members of the Ischnochitonidae. *Sypharochiton* is used for a single species, *S. pelliserpentis* (Quoy & Gaimard, 1835), from southeastern Australia and New Zealand. *Sypharochiton pelliserpentis* exhibits great variation not only in shell and girdle scale morphology, but in the conspicuously polymorphic denticle cap of the major lateral tooth of the radula.

During a study of the polyplacophoran subfamily Chitoninae, it became evident that some members of this group exhibit shell and radular features that suggest ischnochitonid affinities. Conspicuous among this group are species that have at times been placed in the genus *Sypharochiton* Thiele, 1893, and those that have proved to belong to the genus *Radsia* Gray, 1847. The present report utilizes scanning electron microscopy of the girdle scales and dorsal shell surface that has provided information about the usefulness of these phylogenetic characters and the taxonomic status of the species involved.

and radulae. Specimens were prepared for the SEM following the procedures presented by Bullock (1985). The valves were cleaned thoroughly in a heated 2 N solution of KOH, washed several times in distilled water, mounted on aluminum specimen stubs, coated with carbon and gold/palladium in a Denton DV-502 vacuum evaporator, and examined using an ISI MSM-3 SEM located in the Department of Zoology at the University of Rhode Island. Radulae used for light microscopic studies were cleaned, mounted on microslides in Canada balsam, and observed using compound and dissecting microscopes.

Methods and Materials

Specimens of *Radsia* and *Sypharochiton* housed in most major museums of the U.S. East Coast and Europe were examined. Selected specimens were used for light and scanning electron microscopic (hereafter SEM) studies of shell surfaces, girdle scales,

Abbreviations

ANSP Academy of Natural Sciences of Philadelphia
BMNH British Museum (Natural History), London
DMNH Delaware Museum of Natural History, Greenville

IRSN	Institut royal des Sciences naturelles de Belgique, Brussels
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHNP	Muséum national d'Histoire Naturelle, Paris
NMB	Naturhistorisches Museum, Bern
NRS	Naturhistoriska Riksmuseet, Stockholm
RCB	Collection of R. C. Bullock
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden
USNM	National Museum of Natural History, Washington, D.C.
ZMA	Zoölogisch Museum, Amsterdam
ZMHU	Zoologischen Museum, Humboldt-Universität, Berlin
ZMK	Universitetets Zoologiske Museum, Copenhagen

Genus *Radsia* Gray, 1847

Radsia Gray, 1847b:126. Type species by monotypy: *Chiton barnesii* Gray, 1828. *Radsiella* Thiele, 1893:368 [in part].

Description.—Animal reaching 35 mm in length. Lateral triangle with radial sculpture, directed forward. Central areas with numerous longitudinal, beaded, rarely smooth, ribs. Insertion teeth deeply grooved to highly pectinate. Jugal sinus wide. Primary slit-ray consisting of a band of numerous pores; additional pores scattered in posterior depression. Denticle cap of radula elongate, with evidence of 2 cusps, one much more prominent than other; small crystal-like nodules in medial area of larger cusp; central tooth rather broad. Scales dull in appearance, often tan, somewhat squarish, with numerous, fine, irregular striations. Young brooded in branchial groove of female.

Remarks.—The genus *Radsia* and its relationship to other groups of the Chitoninae

which exhibit ancestral characteristics present some of the most interesting and perplexing systematic problems among the Chitonidae. Gray (1847b) first separated *Chiton barnesii* Gray, 1828, from *Chiton* when he introduced the genus *Radsia*, which he characterized by its possession of two slits on each insertion plate, although he had previously described another species, *Chiton capensis* Gray, 1828 [= *Chiton nigrovirescens* Blainville, 1825], which is herein placed in *Radsia*. Earlier in 1847, Gray (1847a) presented a classification of the chitons which provoked the notable conchologist Reeve (1847: pl. 28), but Gray's studies contributed to a much better classification with more natural groupings. But concerning the genus *Radsia*, Gray proposed a useful name for the wrong reason, i.e., two slits on each side of the insertion plate of each intermediate valve. Even Gray (1847b:127) noted that in *Chiton bowenii*, which he evidently considered to be *Chiton* s.s., he found one valve with two slits on one side and "the normal single one of the genus on the other." Unfortunately, the multiple slitting of the insertion plate was considered by conchologists to be the primary characteristic of *Radsia*, and a number of Panamic *Chiton* were placed in *Radsia* by various authors. The natural affinities of *Chiton barnesii* were overlooked because all Panamic species of *Chiton* until now have been placed in *Chiton* s.s.

The recognition of *Radsia* as a natural grouping aids greatly in an evolutionary treatment of the Chitoninae because one can begin to understand the derivation of some shell and radular characteristics intermediate between some *Ischnochiton* groups (family Ischnochitonidae) and species traditionally placed within the Chitonidae. For example, the shovel-like denticle cap of typical chitonid species has an accessory cusp in *Radsia*, an obvious reduction of the second cusp of a bi-cusped, ischnochitonid ancestor. It should be noted that if one were to classify the Polyplacophora solely on the

basis of the radula, *Radsia* would be placed in the Ischnochitonidae. In fact, Thiele (1893, 1909), who emphasized the radula as a phylogenetic tool, placed *R. nigrovirescens* in the genus *Ischnochiton*.

An *Ischnochiton* origin of *Radsia* is evidenced not only by radular characters, but by certain morphological features of the shell. A comparison between *Radsia barnesii* (Gray), the type species of *Radsia*, and *Ischnochiton australis* (Sowerby), the type species of the ischnochitonid subgenus *Ischnoradsia*, illustrates this point. Both species have similar tegmental sculpture, especially since the several "species" of *Ischnoradsia*, which vary greatly in this regard, may in fact be a single species (Leloup 1959). Both *R. barnesii* and *Ischnoradsia* have intermediate valves with a rather thin, multiple-slit insertion plate, and both exhibit a field of pores in the posterior depression on the ventral surface. *Ischnoradsia*, however, has a typical ischnochitonid radula, while that of *R. barnesii*, though not typically chitonid, is similar in some respects to other species of Chitoninae.

An examination of external esthete morphology also confirms the belief that *Radsia* forms a very distinct genus within the Chitoninae. In both *R. barnesii* and *R. nigrovirescens* one finds megalopore-micropore structure unlike other Chitoninae, especially with regard to the collar-like fold surrounding the pores (Figs. 9–12).

In summary, the exact systematic position of *Radsia* is unclear and needs more attention. The species included here have pectinate insertion teeth and a nearly chitonid-like radula, or a radula with a reduced secondary cusp. Excluded species include those with a "definite" *Ischnochiton* radula and/or species with a "definite" *Ischnochiton* insertion plate. There are obvious flaws to such a treatment, but so little material of the questionable species was available for study that such an arrangement was necessary. In any case, the *Radsia* problem poses important questions concerning the validity

of nearly all of the phylogenetic characters presently used by polyplacophoran systematists.

Radsia barnesii (Gray, 1828)

Figs. 2, 4, 6, 7, 11–13, 15, 31, 32

Chiton barnesii Gray, 1828:5 (Coquimbo; type BMNH 1951-1-23.1).—Reeve, 1847: pl. 1, sp. 1.—Pearse, 1979:75, 77 [reproduction].

Radsia barnesii (Gray).—Gray, 1847b:126; 1847c:168.

Chiton (Radsia) barnesii Gray.—Pilsbry, 1893:190, pl. 29, figs. 10–12.—Dall, 1909: 247.—Thiele, 1929:29.—Van Belle, 1978: 20.

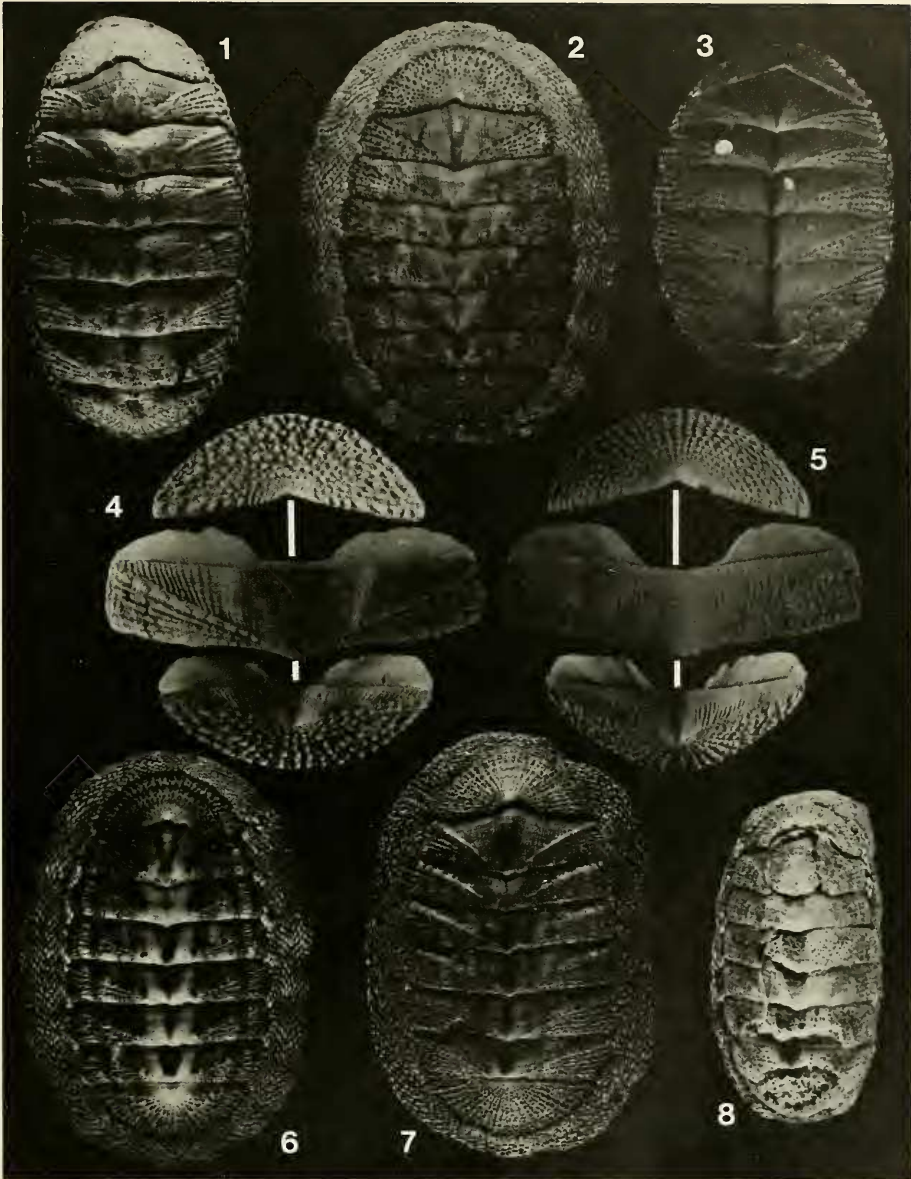
Chiton barnesi Gray.—Plate, 1899:59, pl. 4, fig. 191 [anatomy].—Leloup, 1956:46 [habitat].

Chiton (Radsia) barnesi Gray.—Kaat & Van Belle, 1980:14.

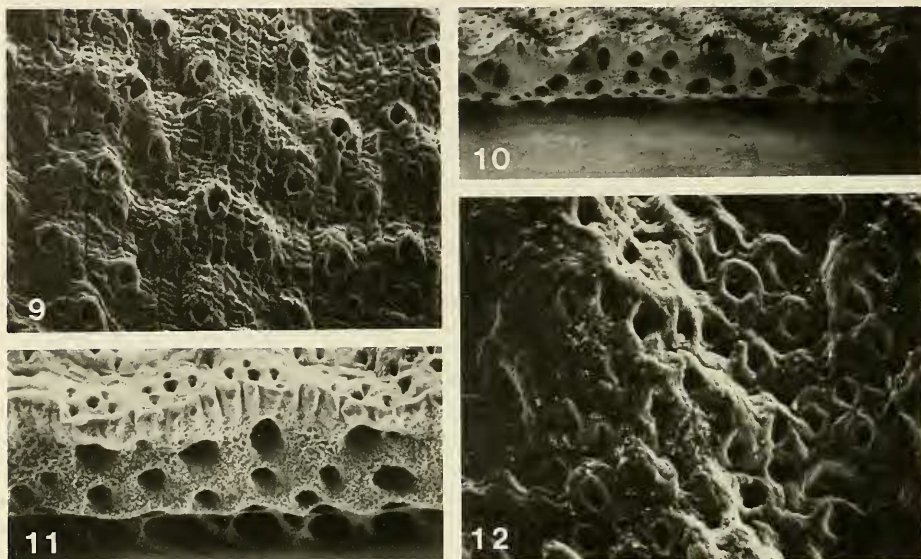
Description.—Animal reaching a length of 35 mm, a width of 26 mm. Valves quite flat, angle about 130°. Anterior valve straight; post-mucral slope of posterior valve straight to slightly concave. Mucro somewhat pointed, anteriorly acentric on posterior valve. Jugal region smooth; central area with numerous uneven longitudinal ribs. Lateral triangle barely raised, with 5–7 irregular nodules. Shell color cream white with reddish brown splotches on central areas, irregular longitudinal dark reddish brown bands on lateral triangles, and occasional dark reddish brown on jugum. Girdle light greenish brown with faint trace of alternating lighter bands in some specimens. Interior of valves white; brownish tegmental color visible in jugal region.

Insertion plates: Apophyses broad, moderately and evenly extended. Intermediate valves multi-slitted, with 2–4 slits per side; insertion teeth deeply pectinate. Anterior valve with 16 teeth; posterior valve with 19–20 teeth.

Tegmentum: Upper layer of suprategmentum thin; lower portion of suprateg-



Figs. 1-8. Shells of *Radsia barnesii* (Gray) and *R. nigrovirescens* (Blainville): 1, Lectotype of *Chiton capensis* Gray [= *R. nigrovirescens*], Cape of Good Hope, 19 mm (BMNH 1951.2.1.9); 2, Holotype of *Chiton barnesii* Gray, Coquimbo, Chile, 35 mm (BMNH 1951.1.23.1); 3, *Radsia nigrovirescens*, Buffels Bay, Cape Point, Port Alfred, South Africa, 14.5 mm (DMNH 16078); 4, *Radsia barnesii*, Cape Choros, Chile, width of intermediate valve 14.3 mm (MCZ 204337); 5, *Radsia nigrovirescens* Buffels Bay, Cape Point, Port Alfred, South Africa, width of intermediate valve 10.3 mm (DMNH 16078); 6, Paratype of *Chiton barnesii* Gray, Coquimbo, Chile, 32 mm (BMNH 1951.1.23.2); 7, *Radsia barnesii*, Cape Choros, Chile, 28.5 mm (MCZ 204337); 8, Syntype of *Chiton nigrovirescens* Blainville, Baie de la Table, 16 mm (MNHNP).



Figs. 9–12. Scanning electron micrographs of esthete pore morphology and anterior tegmental innervation in the genus *Radsia*: 9, 10, *Radsia nigrovirescens* (Blainville), Buffels Bay, Cape Point, Port Alfred, South Africa, 126 \times , 63 \times , respectively (DMNH 16078); 11, 12, *Radsia barnesii* (Gray), Cape Choros, Chile, 126 \times , 252 \times , respectively (MCZ 204337).

mentum enlarged and separated from subtegumentum by thin, esthete-pierced ridge. Suprattegumentum and subtegumentum structurally identical, with small to medium, non-close-packed canals. Close to jugum, subtegumentum differentiated somewhat, composed of slightly larger canals. Suprattegumentum alone on jugum (Fig. 11).

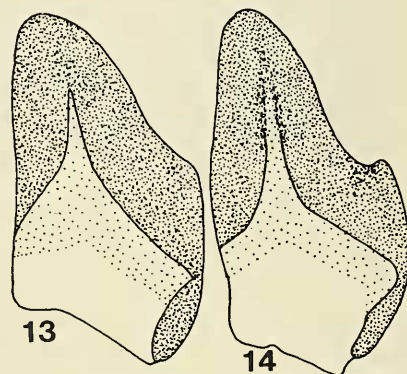
Esthete pores: Megalopores round to ovate, usually situated within a surrounding collar; micropores somewhat smaller, about half diameter of megalopores, more slit-like; most pores connected linearly by obscure anteroposterior crevices (Fig. 12).

Hypostracum: Central depression with few elongate slits, at times more numerous along lateral margins of jugal tract. Primary slit-rays prominent; slits oval to elongate, occasionally a few per longitudinal row. Secondary slit-ray present as field of small esthete holes.

Girdle scales: Moderate in size, roundly triangular, occasionally somewhat pointed; irregular basal reticulations proceed apically as somewhat irregular, variably pro-

nounced ribs, which inturn obliquely and form elongate nodules near apex (Figs. 31, 32).

Radula: Central tooth moderately broad, very concave distally, tapering slightly midway toward base, but widening near base. Pad on centrolateral tooth lacking. Wing of



Figs. 13, 14. Denticle caps of *Radsia*: 13, *Radsia barnesii* (Gray), Cape Choros, Chile (MCZ 204337); 14, *Radsia nigrovirescens*, Buffels Bay, Cape Point, Port Alfred, South Africa (DMNH 16078).



Fig. 15. Known distribution of *Radsia*: *Radsia barnesii* (Gray) (●); *Radsia nigrovirescens* (Blainville) (▲).

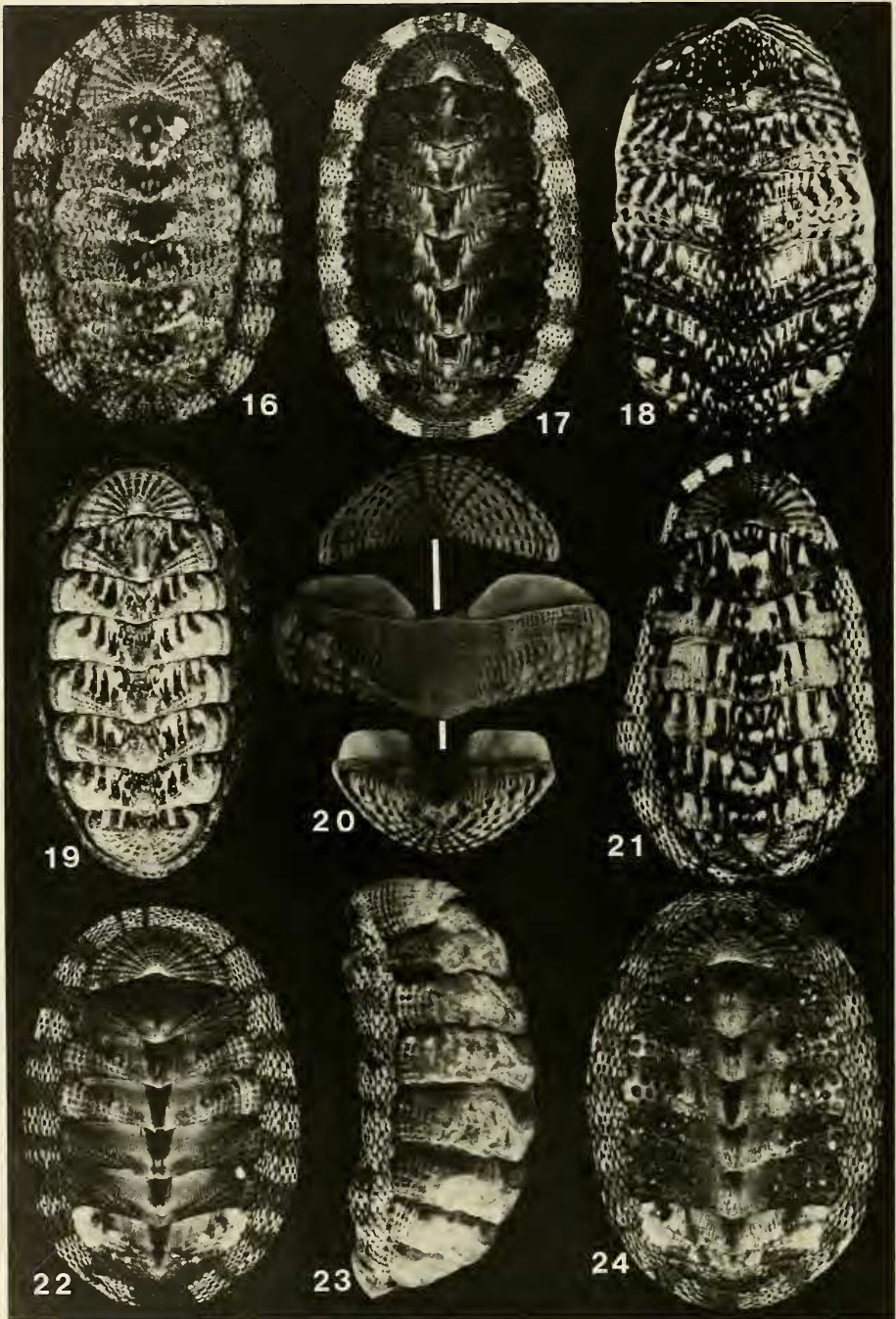
major lateral tooth large, broad, cup-like, with thickened distal edges. Denticle cap elongate, back completely black except for poorly developed channel which extends midway; secondary cusp greatly reduced; primary cusp with black crystal-like nodules coalesced to form elongate black streak beginning at base of channel, widening somewhat as it proceeds distally, and stopping short of tip, except for slight ridge proceeding distally to thin peripheral lip (Fig. 13).

Remarks.—*Radsia barnesii* is closely related to *R. nigrovirescens*, but may be distinguished from the latter by its greenish-brown girdle, which nearly lacks evidence of banding, and shell color pattern, which is often brown speckled with light tan. *Radsia nigrovirescens* is characteristically solid brown, with alternating brown and tan bands on the girdle. The central areas of both species have numerous, narrow longitudinal ribs; *R. nigrovirescens* differs, though, by having these ribs reduced or lacking at the center of the valves. The girdle scales also serve to differentiate these two closely

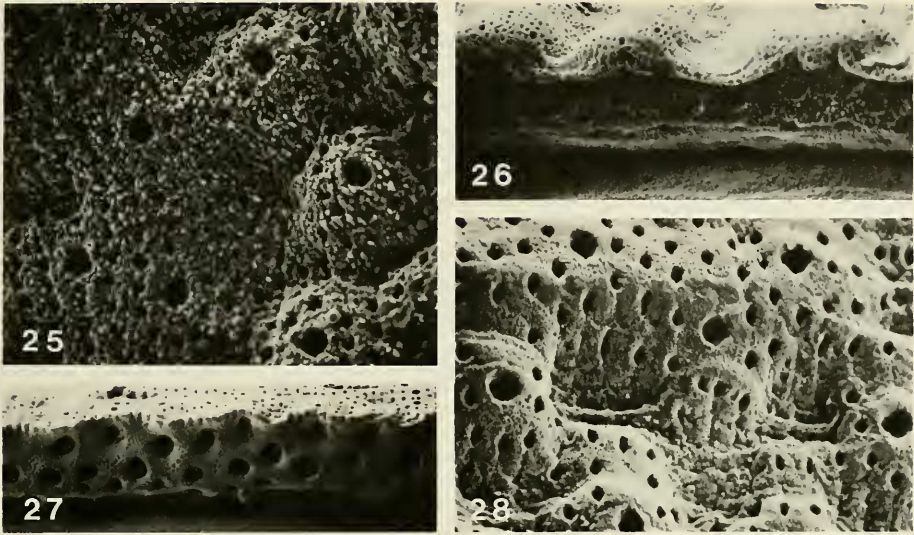
related species: those of *R. nigrovirescens* exhibit a fine reticular pattern over much of the surface; in *R. barnesii* irregular longitudinal ribs are often evident and the reticular sculpture is reduced to the lower ventrolateral area. The radular denticle cap has a greatly reduced secondary cusp which is not as prominent as the secondary cusp in *R. nigrovirescens*.

Radsia barnesii may be confused with *Chiton stokesii* Broderip, 1832, but the lateral triangle of *C. stokesii* is not projected forward as much, and the longitudinal ribbing of the central areas is more prominent. The girdle scales differ significantly: in *C. stokesii* the scales have conspicuous reticular sculpture ventrolaterally and numerous pustules are present apically. *Radsia barnesii* lacks this sculpture. Also, in *C. stokesii* the radular denticle cap differs by lacking any evidence of a secondary cusp and by having a prominent, elongate black tab distally on the back surface.

Aspects of the reproductive biology of both *R. barnesii* and *R. nigrovirescens* afford



Figs. 16–24. Shells of *Sypharochiton pelliserpentis* (Quoy & Gaimard): 16, Kawhia Harbour, New Zealand, 14 mm (ZMK); 17, South Tasmania, 34 mm (MCZ 23160); 18, Little Manly, Auckland, New Zealand, 20.5 mm (USNM 681354); 19, Mt. Manganui, Bay of Plenty, New Zealand, 32.5 mm (DMNH 275511); 20, Taramarama, Sydney, New South Wales, Australia, width of intermediate valve, 12.5 mm (RCB); 21, Little Manly, Auckland, New Zealand, 17.5 mm (USNM 681354); 22, Shellharbour, New South Wales, Australia, 28 mm (MCZ 204350); 23, Syntype of *Chiton pelliserpentis* Quoy & Gaimard, New Zealand, 34 mm (MNHNP); 24, Shellharbour, New South Wales, Australia, 22.6 mm (MCZ 204350).



Figs. 25–28. Scanning electron micrographs of esthete pore morphology and anterior tegmental innervation in *Sypharochiton pelliserpentis*: 25, 26, “*sinclairi*” form, Little Manly, Auckland, New Zealand, 262 \times , 66 \times , respectively (USNM 681354); 27, 28, Tamarama, Sydney, Australia, 262 \times , 66 \times , respectively (RCB).

evidence that the translocation of only one individual could lead to successful colonization. *Radsia barnesii* is known to retain its eggs within the branchial groove until at least the trochophore larval stage (Plate 1897, 1898, 1901). *Radsia nigrovirescens* has been reported to harbor its young in the branchial groove until the final stage of metamorphosis (Thiele 1910, Barnard in Ashby 1931, A. G. Smith 1966). It is interesting to note that these two *Radsia* may be the only Chitoninae known to have non-pelagic larval development. Bullock (in Pearse 1979) reported that “*Chiton*” *torri* Suter, 1907, from Stewart Island, New Zealand, also broods its young. Although Johns (1960, unpublished) examined the type specimen of *C. torri* and stated it to be a juvenile specimen of *Sypharochiton pelliserpentis* (Quoy & Gaimard), the identity of Suter’s species needs to be investigated. *Sypharochiton pelliserpentis* does not brood its young (Johns 1960, unpubl. data) and it is unlikely that *Chiton torri* Suter is conspecific with the former species.

Distribution.—*Radsia barnesii* occurs along the Chilean coast from Coquimbo south to the Chonos Archipelago (Fig. 15).

Material examined.—Chile: (IRSN, NMB); Coquimbo (numerous records); Valparaíso (USNM); Chonos Archipelago (ANSP).

Radsia nigrovirescens (Blainville, 1825)

Figs. 1, 3, 5, 8–10, 14, 15, 29, 30

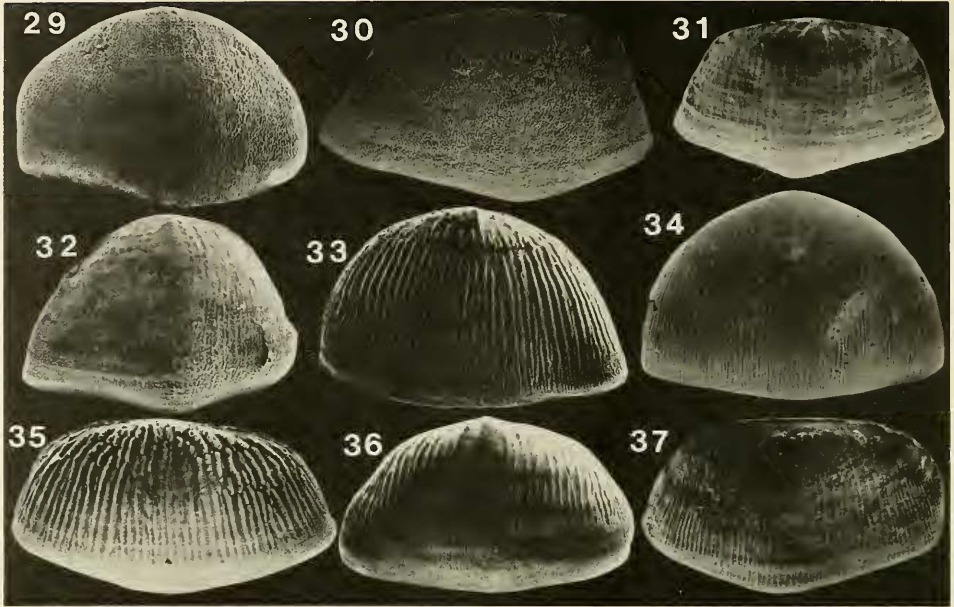
Chiton nigrovirescens Blainville, 1825:538 (Des mers du cap de Bonne-Esperance; type in MNHNP).—Krauss, 1848:38.—Haddon, 1886:22.—Sowerby, 1892:51.—Barnard, 1963:342.—Pearse, 1979:75, 77 [reproduction].—Kaas & Van Belle, 1980:90.

Chiton capensis Wood, 1828:1, pl. 1, fig. 11 (locality unknown; type in BMNH? [not found]). Non Schroter, 1801; nec Gray, 1828.

Chiton capensis Gray, 1828:5 (Cape of Good Hope; type BMNH 1951.2.1.9) [reference to Wood (1828:pl. 1, fig. 11)].—Reeve, 1847:pl. 22, sp. 151.—Krauss, 1848:37.—Sowerby, 1892:51. Non Schroter, 1801; nec Wood, 1828.

Radsia capensis (Gray).—Thiele, 1893:369, pl. 30, fig. 20 [radula].

Chiton nigrovirens [sic] Blainville.—Pilsbry, 1893:187, pl. 31, figs. 41–42.—Sykes,



Figs. 29–37. Scanning electron micrographs of girdle scales of *Radsia* and *Sypharochiton*: 29, 30, *Radsia nigrovirens* Blainville, Buffels Bay, Cape Point, Port Alfred, South Africa, 73×, 85×, respectively (DMNH 16078); 31, 32, *Radsia barnesii* (Gray), Coquimbo, Chile, 37×, 45×, respectively (BMNH); 33, *Sypharochiton pelliserpentis* (Quoy & Gaimard), Island Bay, Wellington, New Zealand, 42× (MCZ 278394); 34, *S. pelliserpentis*, “*sinclairi*” form, Little Manly, North Auckland, New Zealand, 49× (USNM 681354); 35, *S. pelliserpentis*, Shellharbour, New South Wales, Australia, 43× (MCZ 204350); 36, *S. pelliserpentis*, South Tasmania, 35× (MCZ 23160); 37, *S. pelliserpentis*, “*sinclairi*” form, Island Bay, Wellington, New Zealand, 53× (MCZ 278394).

1894:134.—Nierstrasz, 1906:503, figs. 44–49.—Bergenhayn, 1930:29 [shell structure].—Fischer, 1978:46.

Chiton (Lophyrus) capensis Gray.—Clessin, 1904:97, pl. 34, fig. 7 [poor figure].

Ischnochiton nigrovirens [sic] (Blainville).—Thiele, 1909:2; 1910:112.

Chiton (Sypharochiton) nigrovirens [sic] Blainville.—Ashby, 1928:91, pl. 7, fig. 17; 1931:47, pl. 7, figs. 78–81.

Sypharochiton nigrovirens [sic] (Blainville).—Dell, 1962: 513 [brooding behavior]; 1964:121.

Non Georgus nigrovirens [sic] ‘Blainville’ Thiele, 1893: 367 [= *Chiton angusticostatus* Quoy & Gaimard, fide Thiele (1909)].

Description.—Animal moderately small, attaining a length of 25 mm, a width of 15

mm. Valves flattened, angle about 120°. Anterior valve straight to slightly convex. Posterior valve mucro rather blunt, centrally located; post-mucral slope straight. Jugal region granular; central areas granular with numerous irregular longitudinal ribs. Lateral triangle barely raised, with 6–7 uneven, irregularly nodulose, radiating ribs. Terminal areas with numerous such ribs. Shell color dark brown with lighter areas near each mucro. Girdle alternately banded dark brown and reddish tan. Interior of valves light blue, with dull green near apophyses and posterior depression.

Insertion plates: Apophyses moderately extended, slightly more so medially. Jugal sinus broad, trapezoidal; 6–13 irregular, branching jugal teeth, located entirely beneath tegmentum. Intermediate valves with 1–2 slits per side; insertion teeth deeply pec-

tinat. Anterior valve with 16 teeth; posterior valve with 19 teeth.

Tegmentum: Suprategmentum brown, thick, porous, with medium-sized canals; subtegmentum yellowish white, nearly hidden beneath suprategmental overhang, composed of one row of fairly close-packed, larger sized canals (Fig. 10).

Esthete pores: Megalopores round to ovate, located with surrounding collar; micropores about one-third diameter of megalopores, more slit-like; all pores conspicuously connected by anteroposterior crevices (Fig. 9).

Hypostracum: Central depression with number of transverse slits. Primary slit-ray a row of irregular holes. Secondary slit-ray partially developed laterally.

Girdle scales: Relatively moderate in size, roundly triangular, basal reticular sculpture extending dorsally; no trace of lateral ribs except near apex, where some nodes may be present (Figs. 29, 30).

Radula: Central tooth of moderate width, becoming wider basally. Pad on centrolateral tooth not evident. Wing of major lateral tooth large, very conspicuous, with thickened distal edges, cup-like. Denticle cap elongate, back completely black except for poorly developed channel extending midway toward apex; secondary cusp distinctly evident. Back of primary cusp with small, crystal-like nodules medially; distal end smooth, with peripheral swelling forming slight lip, perhaps with low nodule (Fig. 14).

Remarks.—On the basis of the radula and shell morphology, *R. nigrovirescens* is most closely related to *R. barnesii* (Gray) from the west coast of South America, and the two species are herein considered the sole members of the genus *Radsia*. Convincing evidence of this relationship is afforded by the fact that both species have a radular denticle cap that exhibits an obsolete, but still evident, second cusp (Fig. 14; see comparative remarks under *R. barnesii*).

The systematic position of *Radsia nigro-*

virescens has not been discussed fully. Ashby (1928, 1931), who first placed *R. nigrovirescens* in *Sypharochiton*, considered the latter nomen as meriting only subgeneric rank within *Chiton*. Dell (1962, 1964) referred to this species as *Sypharochiton nigrovirens* [sic], because by this time *Sypharochiton* had been raised to full generic rank by Iredale and Hull (1926, 1927) and others, and the subfamily Sypharochitoninae had been mentioned. I believe that *Sypharochiton* should only be used as the genus-group nomen for the type species, *Sypharochiton pelliserpentis* (Quoy & Gaimard). Pilsbry (1893), who stressed shell morphology, placed *R. nigrovirescens* in the genus *Chiton*. On the basis of radular studies, Thiele (1909, 1910) considered *R. nigrovirescens* to be an *Ischnochiton*.

As Barnard (1963) noted, Nierstrasz (1906) questioned the identity of Thiele's *Georgus nigrovirescens* (Blainville), because he observed differences between the radulae of his own specimens and the illustration given by Thiele (1893). Thiele (1909), however, corrected himself, pointing out that his *Georgus nigrovirescens* was, in fact, *Chiton angusticostatus* [= *Rhyssoplax mauritiana* (Quoy & Gaimard), fide Bullock (1972)].

Although a number of authors have "corrected" the spelling of the specific name to "*nigrovirens*," the correct spelling is actually "*nigrovirescens*," as Tomlin (1931) pointed out. It should be noted, however, that both Haddon (1886) and Sowerby (1892) had correctly spelled the name of this species.

Distribution.—*Radsia nigrovirescens* occurs along the South African coast from Saldanha Bay east to Muizenberg (Fig. 15). The Durban locality is highly suspect.

Material examined.—South Africa: Saldanha Bay (ANSP, DMNH, ZMHU); Hoetjes Bay, Saldanha Bay (ANSP); Dassen Is. (RNHL); Robben Is. (ZMHU); Table Bay (IRSN, MNHNP, ZMHU); Cape Town (IRSN, NRS); Sea Point, Cape Town (ANSP,

BMNH, DMNH, ZMA); Oudekraal (BMNH, ZMHU); Muizenberg (ZMA); Durban [Port Natal] (NRS).

Genus *Sypharochiton*
Thiele, 1893

Sypharochiton Thiele, 1893:365. Type species by monotypy: *Sypharochiton pelliserpentis* [sic] (Quoy & Gaimard) [= *Chiton pelliserpentis* Quoy & Gaimard, 1835].

Triboplax Thiele, 1893:366. Type species, to be declared by the ICZN: *Chiton pelliserpentis* Quoy & Gaimard [= *Triboplax scabricula* 'Sowerby' Thiele, non Sowerby, fide Thiele, 1909].

Sympharochiton 'Thiele' Oliver, 1915:558 [spelling error].

Description.—Animal medium to large, reaching a length of 63 mm, valves elevated. Jugal and central regions with numerous incised lines, ribs, or rows of granules; occasionally smooth. Lateral triangle and terminal areas with radiating nodular ribs. Interior of valves yellowish white to blue-green; muscle scars often dark blue-green. Insertion plate of intermediate valves with single slit per side; insertion teeth grooved dorsally. Central depression with a few scattered slits. Denticle cap of major lateral shovel-like, at times with evidence of one secondary cusp on either side of broad central cusp (Figs. 38–49).

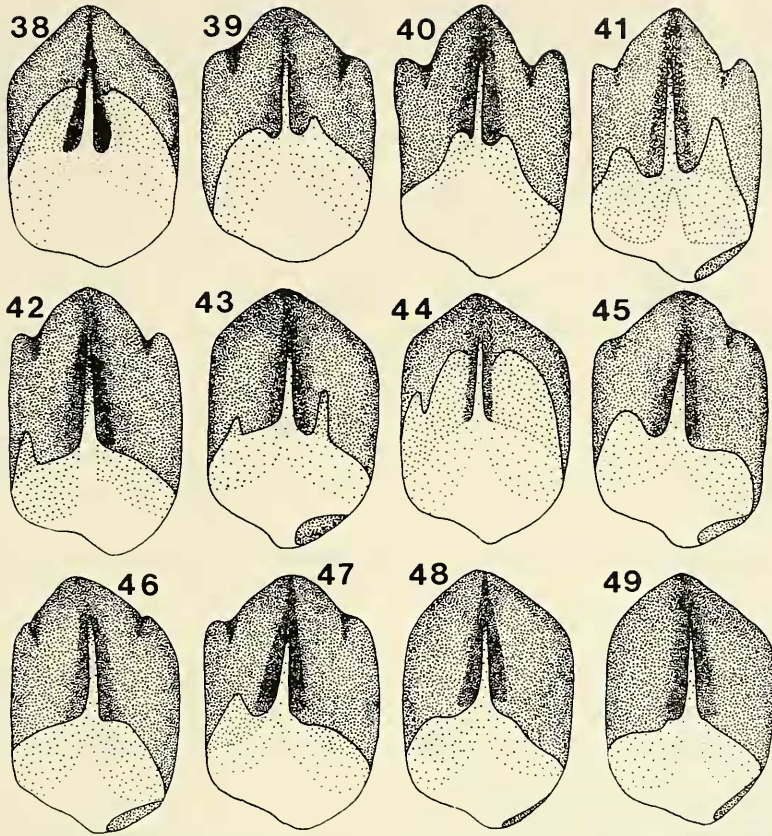
Remarks.—*Sypharochiton* is distinguished from *Radsia* by its more elevated valves and more pronounced radial rows of nodes on the lateral triangle and terminal areas. *Chondroplax*, a subgenus of *Chiton* which has a shell that could be confused with that of *Sypharochiton*, differs from the latter by having widely spaced nodes on the terminal areas and by lacking the conspicuous transverse grooves in the central depression. Each group has distinctly different radular morphology.

As mentioned under the remarks section of *Radsia*, a number of species placed in

Sypharochiton by Iredale & Hull (1926, 1927) have been excluded from the present study because of their definite ischnochitonid affinities. "*Chiton*" *torri* Suter, 1907, broods its young (Bullock in Pearse 1979) and it is unlikely to be conspecific with *S. pelliserpentis* as Johns (1960, unpublished) stated [see remarks under *Radsia*]. Some may properly belong in the Chitoninae, and if so they would be placed in *Radsia*. Davis et al. (1979) published an annotation of an ANSP label for *Chiton iatricus* Winckworth [= *Rhyssoplax peregrina* Thiele] that suggests that this species should be included in *Sypharochiton*. The results of the present study indicate that this is not the case.

The complete acceptance of *Sypharochiton* as a genus-group nomen is not evident in the latest biological literature. Most recent Australian and New Zealand biologists have placed *Chiton pelliserpentis* in the genus *Sypharochiton* (Boyle 1970, 1976; Murdoch & Shumway 1980; Horn 1982; Sakker 1984). However, in an extensive study Johns (1960) utilized *Sypharochiton* at the subgeneric level, and Kaas & Van Belle (1980) did not use *Sypharochiton* in their Catalogue of Living Chitons. The use of *Sypharochiton* is necessary because of the morphological differences between *Sypharochiton pelliserpentis*, the monotypic representative of the genus, and other chitonid genera including *Chiton* and *Radsia*. Radular morphology in particular supports the usefulness of this separation.

There could be some question regarding the type species of *Triboplax* Thiele. *Chiton scabriculus* Sowerby, the name used by Thiele, is not a member of the Chitonidae; Thiele (1909) recognized his mistake and clearly stated that he was working with *Chiton pelliserpentis* at the time that he instituted *Triboplax*. In spite of the obvious solution to this problem, namely to designate *Chiton pelliserpentis* as the type species, the International Code of Zoological Nomenclature stipulates that this situation be referred to the Commission (Art. 70b).



Figs. 38–49. Denticle caps of *Sypharochiton pelliserpentis* (Quoy and Gaimard): 38–40, Tamarama, Sydney, New South Wales, Australia (RCB); 41, Shelly Beach, Manly, Sydney, New South Wales, Australia (RCB); 42, Twofold Bay, Eden, New South Wales, Australia (RCB); 43, 45, Stanley, Tasmania (RCB); 44, Hobart, Tasmania (MCZ 98905); 46–48, Near marine lab, Portobello, Otago Harbour, South Id., New Zealand (RCB); 49, “*sinclairi*” form, Island Bay, Wellington, New Zealand (MCZ 278394).

Sypharochiton pelliserpentis

(Quoy & Gaimard, 1835)

Figs. 16–28, 33–37, 38–50

Chiton pelliserpentis Quoy & Gaimard, 1835:381, pl. 74, figs. 17–22 (Astrolabe Bay, New Zealand; type in MNHNP).—Pilsbry, 1894:85.—Pearse, 1979:63 [reproduction].

Chiton pellis-serpentis [sic] Quoy & Gaimard.—Gray, 1843:246.—Reeve, 1847: *Chiton* pl. 22, sp. 143.—Hutton, 1873:40; 1880:111; 1882:129, pl. 17, fig. 1 [radula].—Haddon, 1886:22.—Cox, 1894:428.—Suter, 1897:195.—Nierstrasz,

1905:86.—Suter, 1913:33, Atlas pl. 2, fig. 12; pl. 4, fig. 6.

Chiton sinclairi Gray, 1843:263 (Great Barrier Island, North Island; type in BMNH).—Reeve, 1847:pl. 22, sp. 143.—Hutton, 1872:176; 1873:40; 1880:111.—Pilsbry, 1893:174, pl. 36, figs. 1–3.—Suter, 1897:195.—Wissel, 1904:627, pl. 23, figs. 38–44; pl. 24, figs. 45–58 [anatomy].—Suter, 1913:35, Atlas pl. 2, fig. 14; pl. 4, fig. 7.—Iredale & May, 1916:115.—Kaas & Van Belle, 1980:120.

Chiton (Lophyrus) pellis-serpentis [sic] Quoy & Gaimard.—von Martens, 1873:36.



Fig. 50. Known distribution of *Sypharochiton pelliserpentis* (Quoy & Gaimard).

- Chiton (Lophyrus) sinclairi* Gray.—von Martens, 1873:36.
- Chiton (Leptochiton) sinclairi* Gray.—E. A. Smith, 1874:pl. 1, fig. 17 [type fig'd.].
- Sypharochiton pellis-serpentis* (Quoy & Gaimard).—Thiele, 1893:366, pl. 30, fig. 12 [radula].—Ashby, 1918:86.—May, 1921:33.—Ashby, 1922:21.—May, 1923:37, fig. 12.—Iredale, 1924:214.—Allan, 1950:238, text-fig. 55, fig. 14a.
- Triboplax scabricula* (Sowerby).—Thiele, 1893:366, pl. 30, fig. 13 [radula]. Non *Chiton scabriculus* Sowerby, fide Thiele (1909).
- Chiton pelliserpentis* [sic] Quoy & Gaimard.—Pilsbry, 1893:173, figs. 14–18.—Leloup, 1952:31, text-fig. 12; pl. 4, fig. 2.—Kaas & Van Belle, 1980:97.
- Chiton (Lophyrus) pellis serpentis* [sic] Quoy & Gaimard.—Clessin, 1903:5, pl. 4, fig. 5.
- Chiton (Lophyrus) sinclairi* Gray.—Clessin, 1903:5, pl. 20, fig. 6.
- Chiton squamosus* Linnaeus.—Wissel, 1904:619, text-fig. F. Non *Chiton squamosus* Linnaeus.
- Chiton (Sypharochiton) pelliserpentis* [sic] Quoy & Gaimard.—Thiele, 1909:2.
- Sypharochiton sinclairi* (Gray).—Iredale, 1915:426.—Iredale & Hull, 1932:153, pl. 10, figs. 1, 2.—Powell, 1937:93, pl. 13, fig. 23.
- Sypharochiton maugeanus* Iredale & May, 1916:114, pl. 5, fig. 6 (Port Arthur, Southern Tasmania; type in Tasmanian Museum, fide Cotton, 1964 [not seen]).—Iredale, 1924:214.—Iredale & Hull, 1926:258, pl. 37, fig. 3; 1927:121, pl. 15, fig. 3.—Cotton & Weeding, 1939:199.—Cotton & Godfrey, 1940:563, fig. 569 [holotype fig'd.].—Allan, 1950:238, text-fig. 55, fig. 14a.—Cotton, 1964:97, fig. 109 [holotype fig'd.].
- Sypharochiton pelli-serpentis maugeanus* [sic] Iredale & May.—Ashby, 1918:86 [spelling error].
- Sypharochiton pellis-serpentis* [sic] *maugeanus* Iredale & May.—Ashby, 1920:579.
- Sypharochiton pellis-serpentis* [sic], var. *sinclairi* (Gray).—Ashby, 1922:579.
- Sypharochiton (Chiton) pellis-serpentis* [sic] (Quoy & Gaimard).—Ashby, 1922:579.
- Sypharochiton pellis-serpentis* [sic] *septentriones* Ashby, 1924:321 (New South

Wales; type in Ashby collection [presumed lost]).

Sypharochiton (Chiton) sinclairi (Gray).—Ashby, 1924:331.

Sypharochiton septentriones Ashby.—Iredale & Hull, 1926:257, pl. 37, figs. 2, 4, 29; 1927:120, pl. 15, figs. 2, 4, 29.—Allan, 1950:238.—Selwood, 1968:71 [reproduction]; 1970:178 [reproduction].

Sypharochiton pelleris (Quoy & Gaimard).—Iredale and Hull, 1926:257; 1927:120; 1932:152, pl. 9, fig. 21.—Powell, 1937:93.—Fleming, 1966:86.—Boyle, 1970:364–384 [ecology].—Luckens, 1974:637–654 [ecology].—Boyle, 1976:382 [esthetes].—Murdoch & Shumway, 1980:128 [oxygen consumption].—Horn, 1982:253 [ecology].—Sakker, 1984:111 [sperm morphology, spermatogenesis, spermiogenesis].

Chiton (Sypharochiton) pelleris-serpentis [sic] Quoy & Gaimard.—Ashby, 1927:108; 1931:47.

Chiton (Sypharochiton) pelleris Quoy & Gaimard.—Johns, 1960:27 [extensive synonymy].

Description.—Animal medium to large in size, reaching a length of 63 mm, a width of 35 mm. Angle of valves variable, 95–110°. Anterior valve and postmucral slope of posterior valve convex. Mucro blunt, centrally located on posterior valve. Jugal and central regions with numerous longitudinal incised lines, ribs, or rows of granules which may not reach preceding valve; at times entire central area smooth. Lateral triangle slightly raised, extending forward, with 3–8 nodular, radiating ribs. End valves with 10–15 nodular, radiating ribs each of which may bifurcate. Shell color variable, often buff or yellowish white with various portions, particularly radial sculpture, dark greenish brown or purplish black. Occasionally some or all valves light or dark. Central areas often with light bluish white or tan. Interior of valves yellowish white to blue-green.

Insertion plates: Apophyses broad, mod-

erately and rather evenly extended. Jugal sinus broad; jugal plate not prominent, grooved dorsally to form varying teeth. Insertion plate of intermediate valves with single slit per side; insertion teeth grooved dorsally, not deeply pectinate. Anterior valve with 13 teeth; posterior valve with 12–16 teeth.

Tegmentum: Suprattegumentum overhanging subtegumentum, composed dorsally of pigmented zone, ventrally of layer of non-close-packed, small, horizontal canals. Subtegumentum of numerous, irregular, small to medium close-packed canals, and fully continuous over jugum. Immature specimens with thick, very porous suprattegumentum and thin subtegumentum composed of single layer of small, non-close-packed canals (Figs. 26, 27).

Esthete pores: Megalopores moderately large, round, about 2–3 times as large as ovate micropores; megalopores often situated individually on mound with surrounding micropores (Figs. 25, 28).

Hypostracum: Central depression with few scattered slits in jugal tract. Posterior portion of central depression and anterior slope of callus with faint grooves, apparently with no slits. Callus developed. Primary slit-ray with numerous small holes, irregularly arranged; mature specimens often with perforated ridge. Posterior depression dull, with numerous scattered small holes, mostly in jugal tract region. Secondary slit-ray similar to primary slit-ray.

Girdle scales: Moderate in size, roundly triangular to nearly rectangular; basal reticular sculpture reduced, somewhat granular; lateral ribs of varying thickness, but constant in single specimen, proceeding apically where they become obsolete or form irregular nodules near apex (Figs. 33–37).

Radula: Central tooth moderately broad; controlateral tooth with conspicuous lateral pad. Major lateral tooth with squarish wing. Denticle cap of major lateral tooth somewhat ovate, back quite black, especially at margins and broad area on either side of distinct medial channel. Secondary cusp,

sometimes very pronounced, may be visible on each side. Primary cusp broad; channel, bordered laterally by ridges, not reaching distal end. Nodules present on back surface on either side of channel, rarely within; distal lip not well formed, formed only at apex (Figs. 38–49).

Remarks.—*Sypharochiton pelliserpentis* most closely resembles *Chiton (Chondroplax) granosus* Fremby, 1827, from Chile, but in *C. granosus* the nodes on the terminal areas of the shell-plates are rather widely spaced, while in *S. pelliserpentis* they are closer together. The radula has a number of significant differences.

Sypharochiton pelliserpentis is a very common species, “often found above neap high water mark” (Iredale & Hull 1927:120). The species exhibits much intraspecific variation. According to previous work by Australian and New Zealand workers, the *S. pelliserpentis* group is composed of two to four species. In addition to *S. pelliserpentis* (Quoy & Gaimard), the names used in the literature of the past few decades include: *S. sinclairi* (Gray, 1843), *S. mauganus* Iredale & May, 1916, and *S. septentriones* Ashby, 1924. Even a preliminary examination of these so-called species indicates that the taxonomy of this group is confusing and that the use of some of the names is inadvisable. Cotton & Godfrey (1940:563) and Cotton (1964:97) stated of *S. mauganus*: “This is the Tasmanian representative of the New Zealand shell *Sypharochiton pelliserpentis* Quoy & Gaimard, and depends upon the geographical locality for status.” Leloup (1952) considered all the forms conspecific, but erroneously included in his synonymy a reference to *Chiton angusticostatus* Quoy & Gaimard because of a comment by Pilsbry, who was uncertain of the latter species’ identity [= *Rhyssoplax mauritiana* (Quoy & Gaimard), a Mascarene islands species (Bullock 1972)].

A rather thorough study by Johns (1960

unpubl. data), published in part by Knox (1963a, 1963b), did not really clarify the entire taxonomic situation. In his study of the ecology and behavioral biology of various populations, Johns found that there is clinal variation in the presence of a black second valve, considered a diagnostic characteristic of Iredale and May’s *Sypharochiton mauganus*, which is now recognized as a junior synonym of *S. pelliserpentis*. The black valve is present in the population at a frequency of 25–40 per cent in the northern portion of its range as compared to 80–90 percent in the south.

The part of Johns’ study that dealt with New Zealand populations proved even more interesting. According to Johns, two forms are observed among the young specimens, which are always found subtidally; these forms are purported to differ in color, sculpture, and the radular ratio. As these animals mature, one form (*S. pelliserpentis*) migrates high into the intertidal zone while the other form (*S. sinclairi*) remains subtidal. The *pelliserpentis* form exhibits homing behavior, certainly an advantageous adaptation for a chiton living in such a habitat, while the *sinclairi* form has not been observed to exhibit homing (Johns in Knox 1963b). Luckens (1974) also observed this difference in homing behavior. Horn (1982: 259) corroborated Johns’ results with regard to the radular ratio and noted that “variations in radular ratios are unlikely to be genetically determined.”

In spite of these differences, which at first suggest that two separate species may be involved, I have concluded that only a single species exists. An examination of the shell and girdle scale morphology of individuals from many populations revealed that morphologically intermediate examples occur. Boyle (1970) arrived at the same conclusion and stated that the two forms are not likely to be reproductively isolated. The differences noted in homing behavior are not unexpected, because there is a gen-

eral tendency for homing behavior in limpets and chitons to be much more pronounced in individuals that live in the intertidal zone. Also, this behavior seems to be totally absent in subtidal populations. Brian & Owen (1952) found that within a population of *Patella vulgata* Linnaeus a difference in the radular ratio obtains, depending on the position in the intertidal zone.

Previous workers have overlooked one intriguing aspect of *S. pelliserpentis* radular morphology. According to Johns (1960:19 unpublished), within the *S. pelliserpentis* group "no differentiation may be made between the species on the form and disposition of the radular teeth." I concur with Johns' conclusion. However, a study of denticle cap morphology, made possible by collections of *S. pelliserpentis* from Australia and New Zealand provided me by Dr. Ruth D. Turner of Harvard University, revealed that the denticle cap of the major lateral tooth of this species is polymorphic (Figs. 38–49). Two extreme forms may occur: one with a prominent secondary cusp on either side of a large, central cusp (Figs. 40–42), the other with no evidence of these secondary cusps (Figs. 38, 43, 48, 49). Various intermediate examples have been found (Figs. 39, 45–47). This polymorphism is found in both Australian and New Zealand localities and is not correlated with the size or sex of the individuals. Although relatively few examples of the *sinclairi* form were available for study, it appears that the radular differences observed do not aid in the separation of these forms.

The genetic basis of denticle cap polymorphism in *S. pelliserpentis* might possibly be an example of paedomorphosis. As noted in the discussion of *Radsia* radular morphology, one likely origin of the broad, single-cusped denticle cap of most chitonids would be a loss of all but the central cusp. O'Neill (1984) observed that in the chitonid *Onithochiton neglectus* Rochebrune the

small juveniles (1.5 mm) have a tricuspid denticle cap, but that with increasing age, the caps quickly assume the typical single-cusped state. Perhaps in *Sypharochiton pelliserpentis* we see varying degrees of retention of a juvenile character; however, radulae of very small *S. pelliserpentis* have not been examined. Other important questions remain, including the relationship between denticle cap form, food sources, and feeding behavior.

The differences in shell morphology, radula, and behavioral ecology of *S. pelliserpentis* may be differentiated into those differences that are environmentally induced (homing behavior, radular ratio), and those that have primarily a genetic basis (shell and girdle scale morphology, denticle cap polymorphism). The present expression of these genetic differences might be explained by secondary intergradation or introgression. Given the geographic isolation of New Zealand and the possibility that gene flow between New Zealand and Australia is greatly restricted (judging from the speciation patterns of the Polyplacophora), one can surmise that incipient speciation could occur in isolated populations of *S. pelliserpentis*. However, this isolation has not been complete, perhaps due to the distances involved, changes in ocean currents, or unknowing translocation of individuals by commercial shipping. Regardless of the origin of this intraspecific variation, it is apparent that individuals of many populations exhibit polymorphic characters and morphological variation, and that the degree of these differences differs from population to population.

Luckens (1974) noted that *S. pelliserpentis* characteristically clears the algae from some areas, while leaving other regions untouched. According to Murray (in Luckens 1974:646): "*Sypharochiton* is an indiscriminate rasping form, and the gut contents include algae, rock particles, crushed barnacle shell and the remains of small crustaceans."

Luckens found that their activity kept the cleared areas devoid of settling barnacles. Most larger intertidal specimens live in a depression in the rock surface to which they exhibit homing behavior (Boyle 1970).

Distribution.—*Sypharochiton pelliserpentis* occurs in New Zealand, New South Wales, and Tasmania (Fig. 50). It has been reported from the Pliocene of New Zealand by Hutton (1886) and Suter (1921). *Sypharochiton* may be extremely abundant, reaching a density of 228/m²; it occurs in a variety of habitats and survives, at least temporarily, in salinities as low as 13.3 ppt and as high as 45.8 ppt (Boyle 1970).

Material examined.—New Zealand: North Island: North Cape (ZMK); Bay of Islands (BMNH); Takapuna (ANSP, BMNH); Auckland (ANSP, IRSN, MCZ, USNM, ZMHU); Ponui Is. (NRS, ZMK); Slipper Is. (ZMK); Tauranga (RNHL); Beacon Reef, Tauranga (DMNH); Mt. Maunganui (ANSP, DMNH); Mahia Peninsula (NRS, ZMK); Wellington (ANSP, BMNH, MCZ, MNHNP); Island Bay, Wellington (MCZ); Karaka Bay, Wellington Harbour (BMNH); under boulders, Opunake (MCZ); New Plymouth (ZMK); Manukau Harbour (MCZ). South Island: Lyttleton (IRSN, NRS, MNHNP); Akaroa (IRSN, NRS, ZMK); Timaru (ANSP); Otago Harbour (MNHNP); Near marine lab., Portobello, Otago Harbour (MCZ, RCB); Foveaux Strait (RNHL); Stewart Is. (ANSP, IRSN); Paterson Inlet, Stewart Is. (NRS, ZMK); Port Pegasus, Stewart Is. (NRS, ZMK); Sumner (RNHL, ZMA, ZMHU). Australia: New South Wales: Sydney (IRSN, USNM); Port Jackson, Sydney (ANSP, BMNH, MCZ, MNHNP, ZMHU); Green Point, Watson's Bay, Port Jackson (ANSP); Bottle and Glass Rocks, Port Jackson (MCZ); Long Reef, Sydney (MCZ, ZMHU); The Spit, Port Jackson (ANSP); Tamarama, Sydney (MCZ, RCB); Shelly Beach, Manly, Sydney (MCZ, RCB); Marouba (BMNH, RNHL, ZMHU); Botany Bay (ZMHU); Shell Harbour (ANSP); Huskisson, Jervis Bay (BMNH);

Cave Bay, Camping ground, Jervis Bay (MCZ); Twofold Bay, Eden (MCZ, RCB). Tasmania: (ANSP); Bridgport (MCZ); Port Arthur (ANSP, MCZ); Frederick Henry Bay (ANSP, ZMHU); Bellerive (BMNH); Hobart (MCZ); Brown's River, mouth of Derwent River (ANSP, NRS); Adventure Bay, South Bruny (MCZ); Robbins Is. (MNHNP, USNM); Stanley (MCZ, RCB).

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Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881.